

## A synthesis of the life history and ecology of juvenile Pacific herring in Prince William Sound, Alaska

BRENDA L. NORCROSS,<sup>1,\*</sup> EVELYN D. BROWN,<sup>1</sup> ROBERT J. FOY,<sup>1</sup> MICHELE FRANDSEN,<sup>1</sup> SHELTON M. GAY,<sup>2</sup> THOMAS C. KLINE, JR.,<sup>2</sup> DORAN M. MASON,<sup>3</sup> E. VINCENT PATRICK,<sup>2,4</sup> A. J. PAUL,<sup>1</sup> AND KEVIN D. E. STOKESBURY<sup>1,5</sup>

<sup>1</sup>Institute of Marine Science, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, PO Box 757220, Fairbanks, AK 99775–7220, USA

<sup>2</sup>Prince William Sound Science Center, PO Box 705, Cordova, AK 99574, USA

<sup>3</sup>National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, 2205 Commonwealth Ave., Ann Arbor, MI 48105, USA

<sup>4</sup>Present address: University of Maryland, Advanced Visualization Laboratory, Computer and Space Science Building, 4423 West College Park, MD 20742, USA

<sup>5</sup>Present address: Center for Marine Science and Technology, University of Massachusetts Dartmouth, 706 South Rodney French Boulevard, New Bedford, MA 02744–1221, USA

### ABSTRACT

Physical and biological variables affecting juvenile Pacific herring (*Clupea pallasii*) in Prince William Sound (PWS) from 1995 to 1998 were investigated as part of a multifaceted study of recruitment, the Sound Ecosystem Assessment (SEA) program. Though more herring larvae were retained in eastern PWS bays, ages-0 and -1 herring used bays throughout PWS as nursery areas. Water transported into PWS from the Gulf of Alaska (GOA) contributed oceanic prey species to neritic habitats. Consequently, variations in local food availability resulted in different diets and growth rates of herring among bays. Summer food availability and possible interspecific competition for food in nursery areas affected the autumn nutritional status and juvenile whole body energy content (WBEC), which differed among bays. The WBEC of age-0 herring in autumn was related to over-winter survival. The limited amount of food consumption in winter was not sufficient to meet metabolic needs. The smallest age-0 fish were most at risk of starvation in winter. Autumn WBEC of herring and winter water temperature were used to model

over-winter mortality of age-0 herring. Differences in feeding and energetics among nursery areas indicated that habitat quality and age-0 survival were varied among areas and years. These conditions were measured by temperature, zooplankton abundance, size of juvenile herring, diet energy, energy source (GOA vs. neritic zooplankton), WBEC, and within-bay competition.

**Key words:** Pacific herring, juvenile fish, feeding, nursery areas, growth

### INTRODUCTION

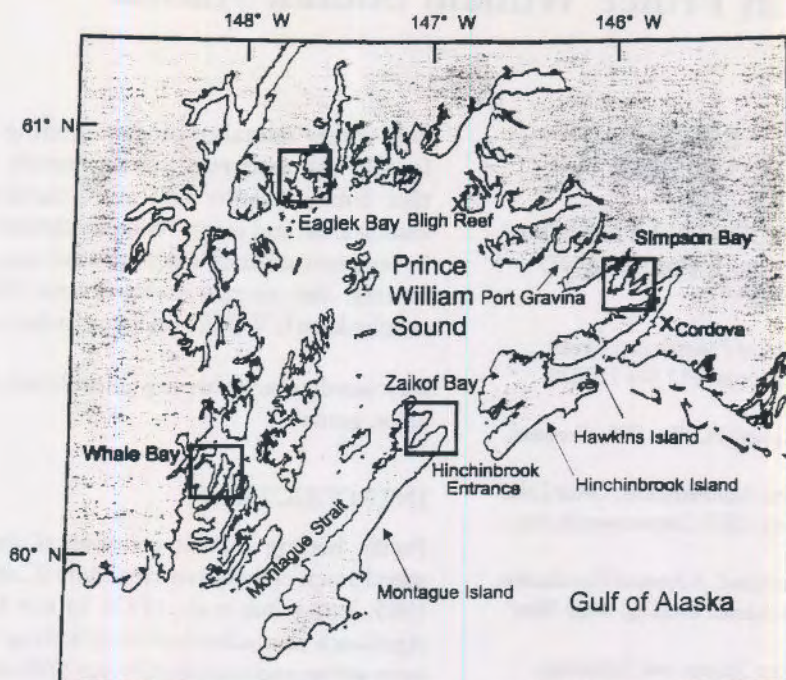
Pacific herring inhabit continental shelf regions and spend much of their lives nearshore (Carlson, 1980; Hay, 1985; Tanisichuk *et al.*, 1993). In late March and early April each year, schools of adult herring begin to migrate from within and outside of Prince William Sound (PWS) (Fig. 1) toward spawning beaches in PWS (J. Wilcock and F. Funk, personal communication, Alaska Department of Fish and Game (ADFG) unpublished data, Juneau AK). Spawning begins by mid-April and lasts from 5 to 21 days. The spawning of herring in PWS is a massive ecological event attended by large aggregations of gulls, shorebirds (see Bishop and Green, 2001; this volume p. 149), humpback whales, and Steller sea lions. Embryonic herring incubate in intertidal and shallow subtidal areas for 22–24 day at ambient temperatures in PWS (Biggs and Baker, 1993; Brown *et al.*, 1996) prior to hatching in May. Though not documented in PWS, pelagic larvae of herring in other Alaskan locations are retained in nearshore nursery areas by local currents (McGurk *et al.*, 1993). During the spring in PWS, adult spawning herring and their offspring are vulnerable to predation, weather patterns, ocean conditions, and human activities.

On 24 March 1989, the tanker vessel Exxon Valdez spilled 42 million litres of crude oil after grounding on Bligh Reef in north-eastern PWS (Fig. 1). From 1 to 20 April 1989, herring spawned over 158 km of shoreline in PWS (Brady *et al.*, 1991). Injury to the PWS Pacific herring population from the Exxon Valdez oil spill was difficult to evaluate because little was known about early life stages (Brown *et al.*, 1996). However, morphologic and genetic damage to larvae and reduced larval growth rates were observed in 1989 (Norcross *et al.*, 1996). It became apparent that we could neither assess the impact of the spill on juvenile herring nor understand processes

\*Correspondence. norcross@ims.uaf.edu



Figure 1. Study area in Prince William Sound, Alaska. Rectangles denote specific bays in which detailed sampling was conducted.



affecting recruitment and restoration of the severely reduced herring population in PWS. The Sound Ecosystem Assessment (SEA) project initiated an integrated, multiinvestigator ecosystem approach in 1994 that continued through spring 1998 (Cooney *et al.*, 2001a; this volume p. 1). The purpose of the SEA herring component was to identify impediments to recruitment during early life history stages of Pacific herring.

Prior to the SEA study, the location of Pacific herring nursery areas in PWS was not known, unlike many North Sea and eastern North America stocks of Atlantic herring (*Clupea harengus*) (Cushing, 1975; Iles and Sinclair, 1982; Sinclair and Iles, 1985). Nearshore areas appear to be important habitat for juvenile Pacific herring in PWS for at least the first year of life (Rounsefell and Dahlgren, 1931). Juvenile herring in British Columbia, Canada, inhabit nursery areas within 1–5 km from shore, often in bays, for up to 2 years (Taylor, 1964; Haegele, 1994; Hay and McCarter, 1997). The proximity of the shore may provide a form of topographical relief required by juvenile herring (Hay and McCarter, 1997). Therefore, we began by examining the nearshore habitat and factors affecting it in PWS.

As part of this integrated research, we identified the life stages and probable factors influencing survival of juvenile herring in PWS through age-0 (first 12 months) and age-1 (second 12 months). Previous research indic-

ated that the effect of prey availability might be reflected in the size, energy content and isotopic signatures of juvenile herring (Kline, 1997; Paul and Paul, 1998a,b). We hypothesized that (i) herring use PWS bays and fjords as nursery areas; (ii) achieving a minimal condition level in summer is critical to over-winter survival of juveniles; (iii) nursery areas vary in quality; (iv) over-winter survival of juvenile herring affects subsequent year-class strength; and (v) the quality of nursery areas affects the nutritional status and year-class strength of herring. Several studies, which measured water temperature and prey abundance, distribution, density, size, growth, diet, isotopic signature, and energy content of juvenile herring, were generated to test these hypotheses and are summarized here.

This review integrates various aspects of juvenile herring research, the details of which have been published in numerous papers, to test the above hypotheses. As a starting point to examining juvenile survival, we summarize the results of other PWS researchers to emphasize the influence of spawning and embryo stages, which in SEA was linked to the juvenile stage through a model of larval drift (Norcross, unpublished data). Combining this information with the results of investigations of factors affecting juvenile survival of herring presents a synthetic view of the ecology and early life history of PWS herring.



## PRE-JUVENILE EFFECTS ON SURVIVAL

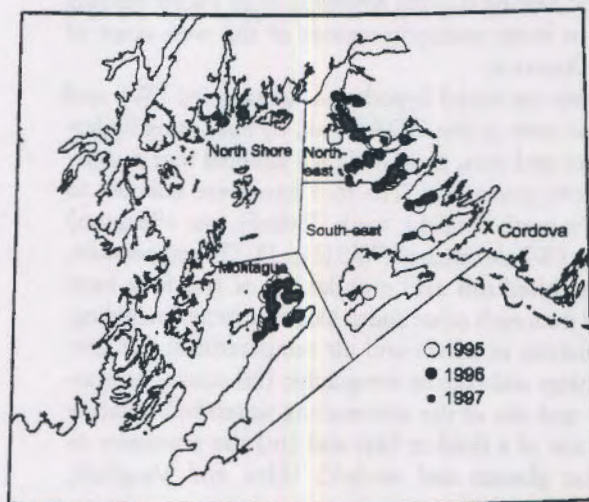
### *Egg deposition and embryo development*

In PWS, readiness to spawn appears to be related to winter and spring sea surface temperatures. PWS herring spawn at water temperatures of approximately 4 °C in calm seas (Biggs and Baker, 1993). Variability in the timing and duration of spawning occurred from 1973 to 1998; mean date of spawn was 20 April  $\pm$  12.3 days (95% CI) (Biggs et al., 1992, J. Wilcock, ADFG, unpublished data). From 1995 to 1998 spawning occurred sequentially earlier (Norcross and Brown, in press) as mean spring water temperatures increased (Gay and Vaughan, 2001; this volume p. 159).

The amount and location of shoreline receiving spawn varied from 1973 to 1998. Aerial surveys estimated a minimum shoreline with spawn of 23 km in 1994 and a maximum of 268 km in 1988 (Brady, 1987; Funk and Hartis, 1992; Funk, 1994). During the SEA study, the total shoreline receiving herring spawn was estimated at 33 km in 1995, 43 km in 1996, and 69 km in 1997 (Willette et al., 1998). The exact spawning locations within PWS varied but were concentrated in the North-east, South-east and Montague regions of PWS (Fig. 2).

The largest source of herring embryo mortality occurs where eggs are physically removed from their substrate by predation or waves (Rooper, 1996). For example, birds in 1994 consumed 27% of the herring eggs deposited (Bishop and Green, 2001; this volume p. 149). Likewise, wave energy may significantly affect egg loss during large storm events (Rooper et al., 1999). Susceptibility to mortality is governed by the depth of egg deposition.

**Figure 2.** Pacific herring spawning locations in Prince William Sound during the SEA project from 1995 to 1997 from ADFG data (Willette et al., 1998).



Embryo mortality in 1995 was estimated at 67–100%, average 75% (Rooper et al., 1999). Other factors such as interannual variability in spawn density and spawning location may also affect egg survival.

### *Dispersal of larvae and juveniles*

Though not documented in PWS, pelagic larvae of herring in other locations are advected away from spawning sites by local currents (Sinclair, 1988). A three-dimensional numerical ocean current model implemented for PWS (3D-PWS model) was used as a tool to study the potential transport of herring larvae from spawning sites to nursery areas. Circulation parameters based on 1996 conditions (Wang et al., 1997, Wang et al., 2001; this volume p. 132) were used to simulate physical dispersal of larvae as passive tracers (Norcross, unpublished data).

The model showed some simulated herring larvae (SHL) advected into bays and retained in PWS, while other SHL were transported from PWS (Norcross, unpublished data). SHL released from all regions were distributed to nearshore areas (Fig. 3). SHL from North Shore, North-east and Montague were transported in a clockwise pattern to the north-east, north, west and south-west, as well as out of PWS through Montague Strait. SHL originating in the South-east (Fig. 3d) had a more limited distribution and were concentrated in the east and north-east; fewer were transported from PWS. Results are consistent with the circulation pattern observed in PWS physical oceanographic studies in 1996 and retention of satellite drifters in the South-east region (Vaughan et al., 2001; this volume p. 58).

The simulated larval transport model demonstrates that herring larvae can be distributed to potential nursery areas (Norcross, unpublished data). Therefore, if passive larval transport determines juvenile distributions, then all nearshore areas of PWS may serve as juvenile nurseries. However, the model could not assess what percentages of larvae were successfully retained in each nursery. The degree to which the circulation in PWS acts as a retention mechanism for herring larvae, and how localized that retention might be, needs further study.

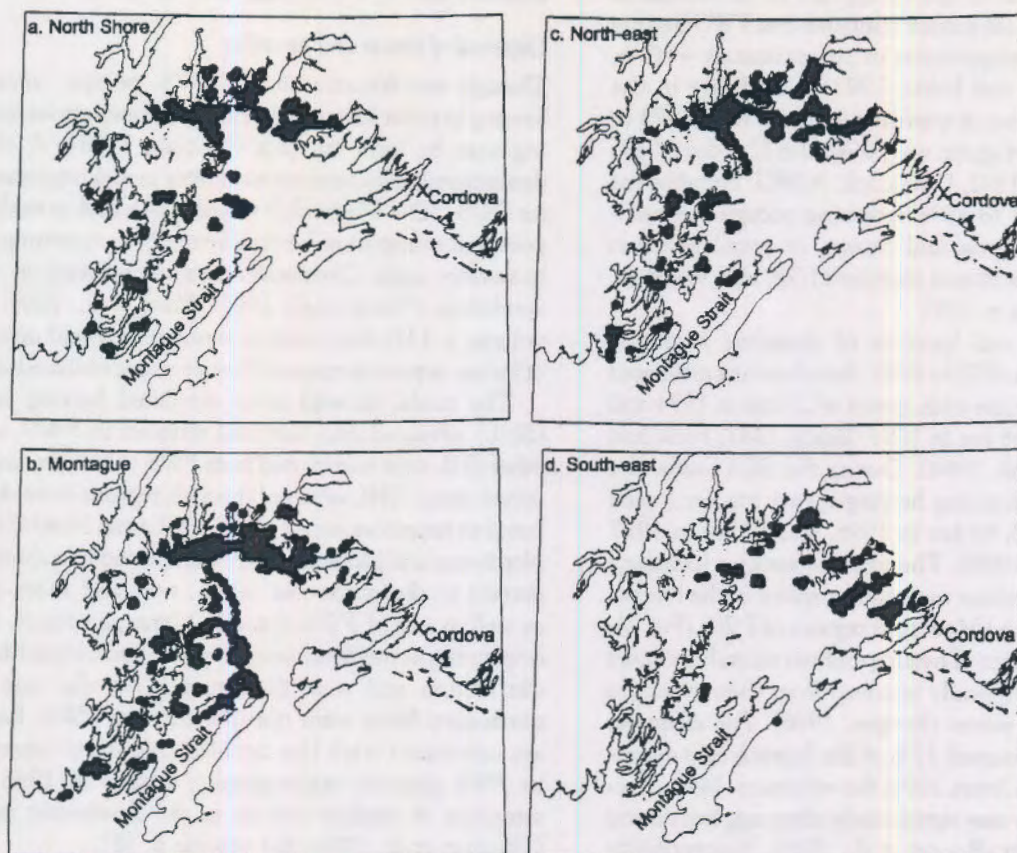
## FACTORS AFFECTING SURVIVAL OF AGE-0 AND AGE-1 JUVENILES

### *Description of nursery areas*

Prince William Sound is a semi-enclosed sea separated from the Gulf of Alaska by a series of mountainous islands (Fig. 1). The rocky coastline has numerous islands, inlets, bays, and deep fjords. About half of the locations sampled during this study, though named and referred to as bays, were classified as small fjords. These



**Figure 3.** Herring spawning regions in 1996 and dispersal of simulated herring larvae (SHL) hatched in those regions: (a) North Shore, (b) Montague, (c) North-east, and (d) South-east. Egg deposition sites from ADFG aerial surveys (Willette *et al.*, 1998) were used as starting locations for SHL transport (black). Cumulative (without mortality) dispersal patterns of SHL from spawning region of origin as of 1 July 1996 (grey).



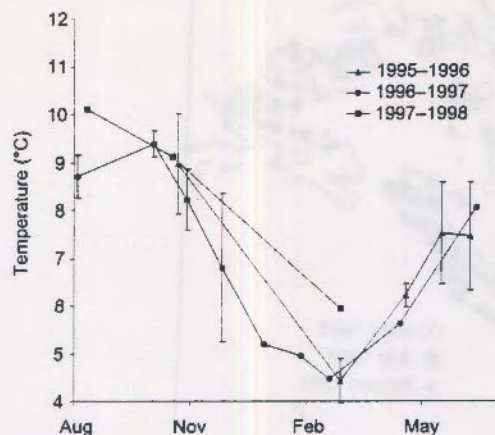
fjords are characterized as steep-sided basins with maximum depths over 100 m; entrance sills varying in depth were present in some but not all fjords. Fjords generally have slow tidal currents ( $< 15 \text{ cm s}^{-1}$ ) and are stratified during periods of freshwater runoff. By late winter, the subsurface and deep waters are well mixed, but the surface layers can exhibit slight stratification. Other shallower ( $< 100 \text{ m}$ ) locations classified as bays are more prone to vertical mixing from both winds and strong tidal currents. Bays may exhibit partial to strong stratification briefly during the summer. In comparison with fjords, by early autumn bays are typically well mixed vertically, and by late winter their water columns become homogeneous from surface to bottom. Thermal conditions from 1995 to 1998 were cold and relatively well-mixed during late winter ( $4\text{--}6^\circ\text{C}$ ) followed by stratification ( $9\text{--}13^\circ\text{C}$ ) in the summer (Gay and Vaughan, 2001; this volume p. 159). At  $60^\circ\text{N}$ , primary production in PWS is typical for high latitude neritic systems with a strong spring phytoplankton bloom (McRoy *et al.*,

1997) and a short growing season. In this northern location, the combination of light and temperature restrictions create environmental conditions for Pacific herring that are somewhat different from those experienced by Atlantic herring (*Clupea harengus*) or by Pacific herring found in more southerly regions of the west coast of North America.

To test our stated hypotheses, we sampled PWS and adjacent areas in the GOA by air, by boat using hydroacoustics and nets, and finally we sampled four nursery bays more intensively. The four bays were selected to represent north (Eaglek), south (Zaikof), east (Simpson) and west (Whale) areas of PWS (Fig. 1). The temperature, salinity, plankton and circulation of the four bays differed from each other due to localized factors including: (i) variation in winds and air temperatures; (ii) geomorphology and bottom topography; (iii) coastal oceanography and size of the surrounding watersheds relative to the size of a fjord or bay; and (iv) the proximity to tidewater glaciers and ice-fields (Gay and Vaughan,



**Figure 4.** Water temperature (and standard deviation) at 25 m averaged over all sites in four bays sampled August 1995–March 1998. Standard deviation bars plotted for all but not visible when smaller than symbol.



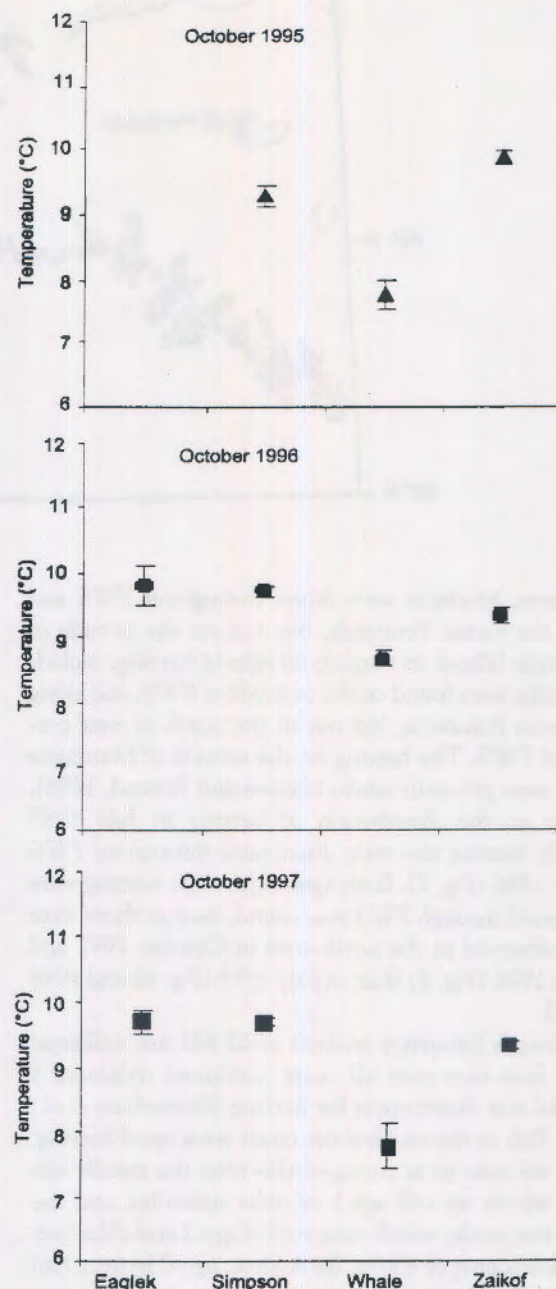
1998; 2001; this volume p. 159). Eaglek Bay is a classic fjord with a sill depth of 50–100 m and a basin depth of 200 m. Whale Bay is an unsilled fjord with a basin depth of 280 m. Zaikof and Simpson Bays are not fjords and have basin depths of 90 m and 100 m, respectively. These bays were surveyed 12 times from October 1995 to March 1998 (Stokesbury *et al.*, 1999, 2000; in press). The average water temperatures in PWS bays taken at 25 m displayed seasonal and interannual patterns (Fig. 4). Though March is the coldest month, it was significantly warmer in 1998 than in other years. In addition to interannual average-temperature differences, there were also interannual temperature differences within and between bays as demonstrated for October (Fig. 5).

#### *Distribution, relative density, length, and growth*

To adequately sample the bays both horizontally and vertically, fish were sampled using several types of nets: a modified trawl for deep water collection, an anchovy seine for large surface schools and a small salmon fry seine for shallow water fishes (Stokesbury *et al.*, 1999, 2000). Fish were also surveyed acoustically along standardized transects.

Results from seasonal PWS-wide net, acoustical (Stokesbury *et al.*, 2000) and aerial (Brown *et al.*, 1999) surveys (1995–96) and historical (1934–98) analysis (Brown *et al.*, in press), supported the first hypothesis that bays and fjords throughout PWS were herring nursery areas throughout the year. The aerial surveys (Brown and Borstad, 1998) for 3 months in summer 1995 within PWS and adjacent areas indicated that juvenile herring were broadly distributed in nearshore bays (Fig. 6). The within-summer distribution revealed some differences in age composition and distribution patterns of schools. In

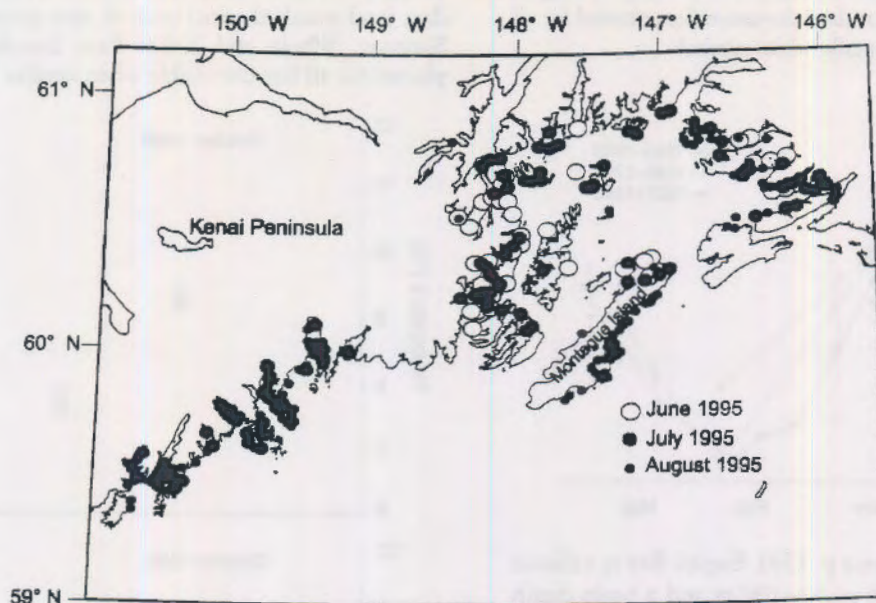
**Figure 5.** Water temperature at 25 m in Prince William Sound in October 1995, 1996 and 1997. Points are average data (and standard error) over all sites sampled in Eaglek, Simpson, Whale and Zaikof Bays. Standard error bars plotted for all but not visible when smaller than symbol.



June, before age-0 fish had metamorphosed and when mostly age-1 fish occupied the bays, aerial surveys found almost no juveniles outside of PWS along the Kenai Peninsula (Fig. 6). In July, when the new year class was entering bays, schools included both ages-0 and -1. At



**Figure 6.** Locations of Pacific herring schools in Prince William Sound and along the Outer Kenai Peninsula during 1995 aerial surveys: June, age-1; July, age-0 and -1; and August, age-0, -1 and  $\geq 2$ .



that time, juveniles were found throughout PWS and along the Kenai Peninsula, but not on the outside of Montague Island. In August, all ages of herring, including adults, were found on the east side of PWS, and along the Kenai Peninsula, but not in the north or west portions of PWS. The herring on the outside of Montague Island were primarily adults (Brown and Borstad, 1998). Similar to the distribution of herring in July 1995 (Fig. 6), herring also were distributed throughout PWS in July 1996 (Fig. 7). Both ages of juvenile herring were distributed through PWS year round, though there were fewer observed in the north-west in October 1995 and March 1996 (Fig. 8) than in July 1995 (Fig. 6) and 1996 (Fig. 7).

A length frequency analysis of 63 981 fish collected in the four bays over all years combined indicated a trimodal size distribution for herring (Stokesbury *et al.*, 1999). Fish in the smallest size mode were age-0 herring, which we refer to as young-of-the-year; the middle size mode, which we call age-1 or older juveniles; and the largest size mode, which consisted of age-2 and older herring adolescents or adults. By August, age-0 herring had entered the nursery areas; thus, August is the beginning point of our portrayal of juvenile life history (Fig. 9). Lengths of both juvenile year classes increased rapidly from August to October, but showed little growth over the winter (Fig. 9a). The relative density of age-0 herring within bays, as determined by acoustic sampling, usually decreased after July or August of each year (Table 1).

Apparent increases or decreases in relative density of juvenile herring may be explained by differential size-specific migration of juvenile herring within and among bays. Older juveniles migrate out of the bays in the summer (Stokesbury *et al.*, 2000) as the new year class of herring is transported into the nursery areas. Drifters moving among bays within a region (Vaughan *et al.*, 2001; this volume p. 58), indicate potential physical circulation patterns that could assist actively swimming juvenile herring in migration to nearby bays. Confirmation of migration of juveniles at other times would require a large-scale tag/recovery effort.

The average length of age-0 herring varied among years (Fig. 9a). The average size of age-0 and -1 herring in August was smaller in 1996 than at the same time in 1997. In 1996, July and August water temperatures were cooler than in 1997 (Fig. 4; Gay and Vaughan, 2001; this volume p. 159). Prior to these collections, the May 1996 biomass of zooplankton was similar to that of 1997, while the July 1996 zooplankton biomass ( $0.47 \text{ g m}^{-2}$ ) was significantly higher than in July 1997 ( $0.22 \text{ g m}^{-2}$ ; Fig. 9b). Due to lack of June sampling in 1997, we were not able to establish whether this difference between years was due to a difference in zooplankton abundance or a difference in timing of zooplankton reproduction, either of which may have resulted from the lower production of phytoplankton in 1997 (Eslinger *et al.*, 2001; this volume p. 81). Increased spring and summer water temperatures



Figure 7. Herring distribution observed by acoustic and aerial surveys in July 1996. Acoustic surveys report herring schools by age class. Aerial surveys report herring by size of school (Brown and Borstad, 1998).

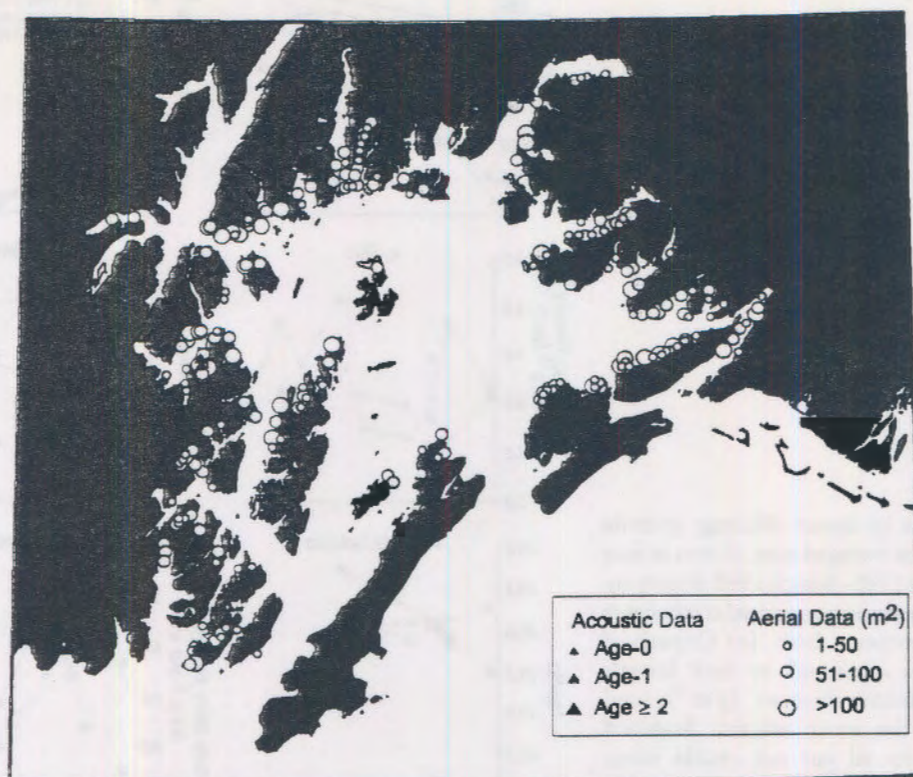
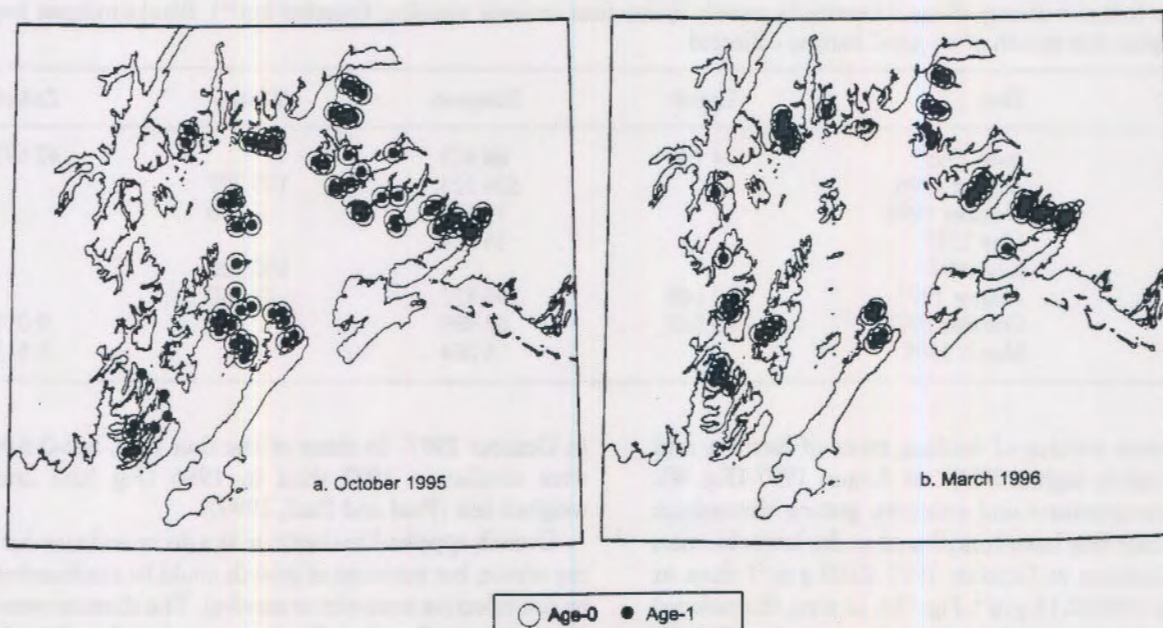
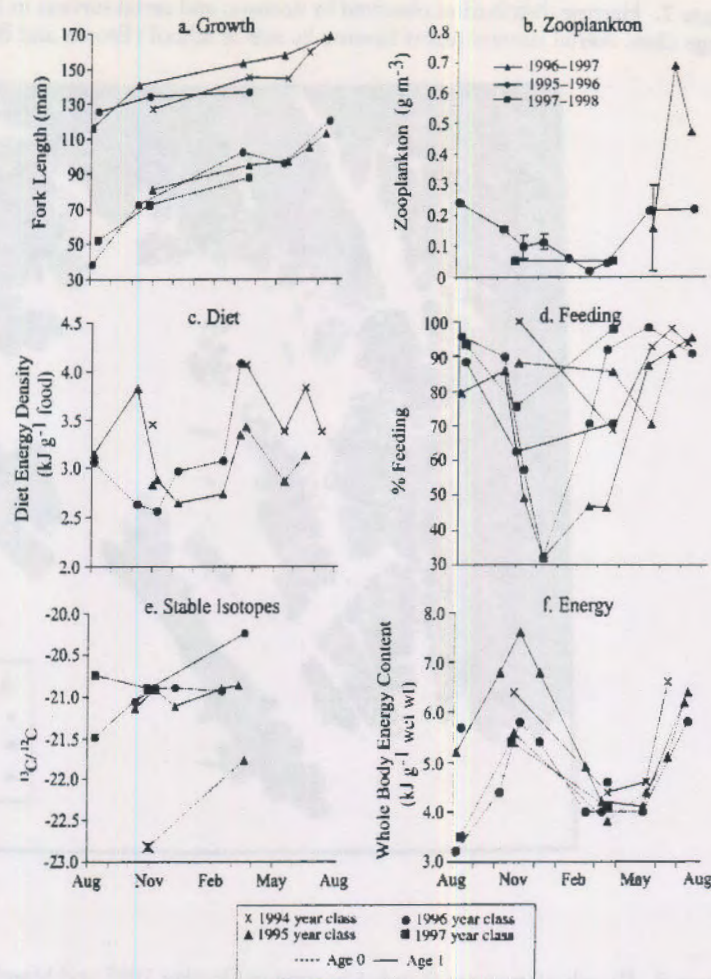


Figure 8. Distribution of age-0 and -1 herring in October 1995 and March 1996 as detected acoustically and collected with nets.







**Figure 9.** Composite of factors affecting juvenile herring in PWS. Data averaged over all sites in four bays sampled August 1995–March 1998. Points are not connected when important seasonal components were not sampled between them. (a) Growth of juvenile herring, as measured by fork length (mm). (b) Zooplankton biomass ( $\text{g m}^{-3}$ ) (and standard error) in the water column. Standard error bars plotted for all but not visible when smaller than symbol. (c) Estimated diet energy density ( $\text{kJ g}^{-1}$  food). (d) Percentage of juvenile herring with food in stomachs. (e) Stable isotopes ( $^{13}\text{C}/^{12}\text{C}$ ). (f) Whole body energy content of juvenile herring ( $\text{kJ g}^{-1}$  wet weight).

**Table 1.** Relative density of age-0 herring by month by bay from acoustic sampling (number  $\text{km}^{-2}$ ). Blanks indicate bay not sampled that month or no age-0 herring collected

Cohort	Date	Eaglek	Simpson	Whale	Zaikof
1996	June 1996	24 195	66 473		47 692
1996	August 1996		524 123	105 707	
1996	October 1996		11 665	2 536	
1996	May 1997		16 429		
1997	July 1997			150 528	
1997	August 1997	10 149	296 572	28 240	
1997	October 1997	15 518	62 989		9 017
1997	March 1998		5 064		1 513

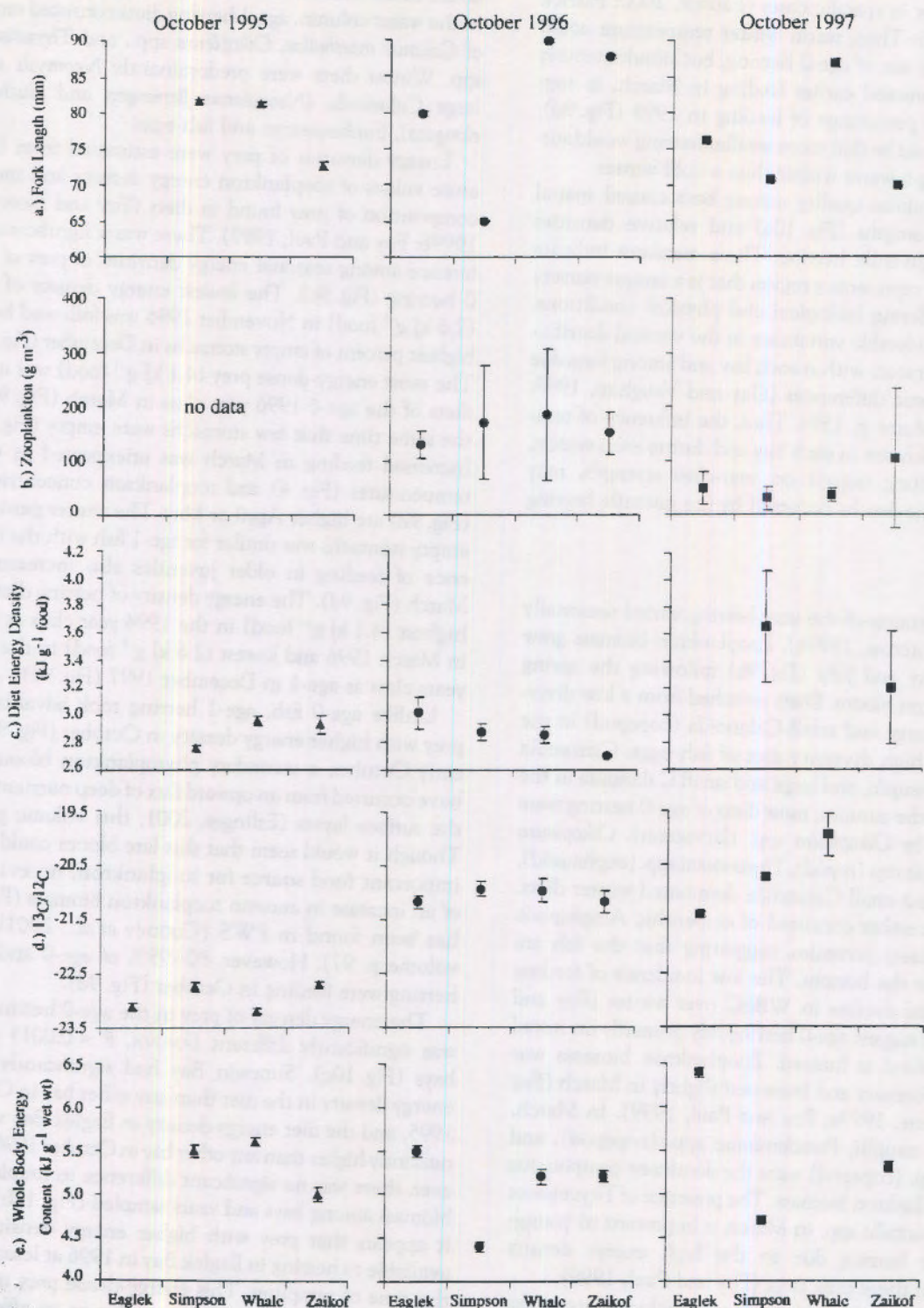
could have enhanced feeding rates of herring and led to slightly higher WBEC in August 1997 (Fig. 9f). Warm temperatures and excessive grazing throughout the summer may have contributed to the lower biomass of zooplankton in October 1997 ( $0.05 \text{ g m}^{-2}$ ) than in October 1996 ( $0.15 \text{ g m}^{-2}$ ; Fig. 9b). In turn, the reduced prey availability may be reflected in growth reduction

in October 1997. In three of the four bays, age-0 fish were smaller in 1997 than in 1996 (Fig. 10a) and weighed less (Paul and Paul, 1999).

Growth appeared to continue at a decreased rate during winter, but measures of growth could be confounded by size-selective over-winter survival. The shortest over-wintering age-0 and -1 herring were found in March



**Figure 10.** Composite of factors affecting age-0 herring in Prince William Sound in October 1995, 1996 and 1997. Points are average data (and standard error) over all sites sampled in Eaglek, Simpson, Whale and Zaikof Bays. Standard error bars plotted for all but not visible when smaller than symbol. (a) Growth of juvenile herring, as measured by fork length (mm). (b) Zooplankton biomass ( $\text{g m}^{-3}$ ) integrated over the water column. (c) Estimated diet energy density ( $\text{kJ g}^{-1}$  food). (d) Stable isotope ratios ( $^{13}\text{C}/^{12}\text{C}$ ). (e) Whole body energy content of juvenile herring ( $\text{kJ g}^{-1}$  wet weight).





1998 (Fig. 9a), when the spring temperature was significantly warmer (ANOVA,  $P < 0.001$ ) than the two previous years (Fig. 4). Warmer winter temperature may cause increased metabolic demands though it does not affect survival except in specific cases (Patrick, 2000; Patrick *et al.*, in press). Thus, warm winter temperature could reduce average size of age-0 herring, but simultaneously may have promoted earlier feeding in March, as suggested by the percentage of feeding in 1998 (Fig. 9d). The result would be that more smaller herring would survive following a warm winter than a cold winter.

Variable habitat quality among bays caused spatial variation in lengths (Fig. 10a) and relative densities (Table 1) of juvenile herring. These measures indicate that each bay represents a region that is a unique nursery area with differing biological and physical conditions. There is considerable variability in the vertical distribution of temperature within each bay and among bays due to characteristic differences (Gay and Vaughan, 1998; 2001; this volume p. 159). Thus, the influence of temperature on fish size in each bay and during each season, and its resulting impact on year-class strength, may depend on the depths occupied by the juvenile herring in that bay.

#### Diet

The diet of young-of-the-year herring varied seasonally (Foy and Norcross, 1999b). Zooplankton biomass grew between May and July (Fig. 9b) following the spring phytoplankton bloom. Diets switched from a low diversity diet of large and small Calanoida (copepod) in the spring to a high diversity diet of fish eggs, Cirripedia (barnacle) nauplii, and large and small Calanoida in the summer. In the autumn, most diets of age-0 herring were dominated by *Oikopleura* spp. (larvacean), *Oikopleura* spp., *Neomysis rayi* (mysid), *Thysanoessa* spp. (euphausiid), and large and small Calanoida dominated winter diets. Prey in December consisted of epibenthic Amphipoda and Polychaeta juveniles, suggesting that the fish are feeding near the bottom. The low incidence of feeding (Fig. 9d) and decline in WBEC over winter (Foy and Paul, 1999) suggest age-0 herring rely primarily on stored energy as food is limited. Zooplankton biomass was lowest in February and increased slightly in March (Foy and Norcross, 1999a; Foy and Paul, 1999). In March, Cirripedia nauplii, *Pseudocalanus* spp. (copepod), and *Metridia* spp. (copepod) were the dominant components of the zooplankton biomass. The presence of *Thysanoessa* spp. and *Metridia* spp. in March is important to young-of-the-year herring due to the high energy density (Fig. 9c) of these prey taxa (Foy and Paul, 1999).

Prey consumed by older juveniles included larger taxa in addition to those consumed by young-of-the-year

herring. Spring diets of age-1 herring were comprised of large Calanoida (*Neocalanus cristatus* and *Metridia okhotsensis*) and Cirripedia nauplii. Summer diets contained mostly Euphausiacea juveniles, fish eggs and small Calanoida. In the autumn when *Oikopleura* spp. were abundant in the water column, age-1 herring diets consisted mostly of *Calanus marshallae*, *Oikopleura* spp., and *Thysanoessa* spp. Winter diets were predominantly *Neomysis* spp., large Calanoida (*Neocalanus flemingeri* and *Euchaeta elongata*), Euphausiacea and fish eggs.

Energy densities of prey were estimated from literature values of zooplankton energy density and species composition of prey found in diets (Foy and Norcross, 1999b; Foy and Paul, 1999). There was a significant difference among seasonal energy densities of prey of age-0 herring (Fig. 9c). The lowest energy density of prey ( $2.6 \text{ kJ g}^{-1}$  food) in November 1996 was followed by the highest percent of empty stomachs in December (Fig. 9d). The most energy-dense prey ( $4.1 \text{ kJ g}^{-1}$  food) was in the diets of the age-0 1996 year class in March (Fig. 9c) at the same time that few stomachs were empty (Fig. 9d). Increased feeding in March was unexpected as water temperatures (Fig. 4) and zooplankton concentrations (Fig. 9b) are higher April or May. The winter pattern of empty stomachs was similar for age-1 fish with the incidence of feeding in older juveniles also increasing in March (Fig. 9d). The energy density of herring diets was highest ( $4.1 \text{ kJ g}^{-1}$  food) in the 1994 year class as age-1 in March 1996 and lowest ( $2.6 \text{ kJ g}^{-1}$  food) in the 1995 years class as age-1 in December 1997 (Fig. 9c).

Unlike age-0 fish, age-1 herring took advantage of prey with higher energy density in October (Fig. 9c). In early October, a secondary phytoplankton bloom may have occurred from an upward flux of deep nutrients into the surface layers (Eslinger, 2001; this volume p. 81). Though it would seem that this late bloom could be an important food source for zooplankton, no evidence of an increase in autumn zooplankton biomass (Fig. 9b) has been found in PWS (Cooney *et al.*, 2001b; this volume p. 97). However, 80–95% of age-0 and age-1 herring were feeding in October (Fig. 9d).

The energy density of prey in the age-0 herring diets was significantly different (ANOVA,  $P < 0.001$ ) among bays (Fig. 10c). Simpson Bay had significantly lower energy density in the diet than any other bay in October 1995, and the diet energy density in Eaglek Bay was significantly higher than any other bay in October 1996. However, there was no significant difference in zooplankton biomass among bays and years sampled (Fig. 10b). Thus it appears that prey with higher energy density were available to herring in Eaglek Bay in 1996 at least during the time of sampling. This energy-dense prey may not have been available in Simpson Bay or its effect may



have been limited by greater densities of juvenile herring and therefore increased grazing competition. The diet energy density was significantly higher in 1997 (ANOVA,  $P < 0.05$ ) than previous years (Fig. 10b) when herring had fewer medium and small Calanoida (lower energy density) in their diets. The zooplankton biomass was significantly lower (ANOVA,  $P = 0.015$ ) in October 1997 than in 1996 (Fig. 10b). Thus, despite the high energy density of the prey, the reduced availability of prey in 1997 may have contributed to the small sizes of herring found in three of the four bays (Fig. 10a). Prior to overwintering, quantity of food may be more important than quality of food and a reduction in food has potential to decrease survival of juvenile herring.

#### Stable isotopes

To examine another aspect of the quality of food, the source of herring food was examined, i.e. the proportion of allochthonous production of zooplankton occurring outside of PWS and available to juvenile herring. Differences in  $^{13}\text{C}/^{12}\text{C}$  between PWS and the adjacent GOA plankton distinguish the principal sources of carbon in PWS biota (Kline, 1997, 1999a, 1999b). Stable isotope ratios in food webs provide a convenient means for showing trophic linkages because of their conservative transfer. A subset of the same fish used for WBEC analysis was analysed for natural stable isotope proportions (Kline, 1999a).

There are several key observations and implications of the  $^{13}\text{C}/^{12}\text{C}$  analyses for understanding juvenile herring ecology. With the sole exception of spring 1996, during 1994–97, carbon from the GOA had more negative  $^{13}\text{C}/^{12}\text{C}$  than carbon in PWS (Kline, 1999b). Differences in  $^{13}\text{C}/^{12}\text{C}$  were found among year classes of herring (Fig. 9e). More negative  $^{13}\text{C}/^{12}\text{C}$  values were observed in age-0 1995 year class and age-1 1994 years class herring in 1995 (Fig. 9e) than in the other years of the study (Kline, 1999a). Individuals with a more negative  $^{13}\text{C}/^{12}\text{C}$  GOA signature (Kline, 1999a; Cooney et al., 2001b; this volume p. 97) dominated the population of the copepod *Neocalanus cristatus* that underwent diapause in PWS in autumn 1995. Zooplankton in PWS in 1995 had the most negative  $^{13}\text{C}/^{12}\text{C}$  signatures observed during the years 1994–97 (Kline, 1999b). These observations are consistent with the hypothesis that there was an influx of carbon from the GOA into PWS in 1995. However, this different source of food for herring in 1995 did not appear to affect growth (Figs 9a and 10a).

The interannual shifts in  $^{13}\text{C}/^{12}\text{C}$  values in herring were much greater than the differences among bays in October (Fig. 10d). When considering ages-0 and -1 values of  $^{13}\text{C}/^{12}\text{C}$  in October, the difference between 1995 and both 1996 and 1997 were significant (Scheffe,

$P < 0.001$ ), whereas there were no significant differences among bays. Though the diet composition was not different, stable isotopes indicate that the food source herring consumed in PWS prior to October 1995 was principally from sources outside PWS. Thus, physical transport mechanisms were responsible for delivery of food to herring nursery areas. During October of a single year, the relatively small differences in  $^{13}\text{C}/^{12}\text{C}$  among the four bays suggest that effects of variability in the GOA influx may be pervasive within PWS. Small  $^{13}\text{C}/^{12}\text{C}$  gradients within PWS may reflect influx pathways. For example, the most negative  $^{13}\text{C}/^{12}\text{C}$  values in autumn 1995 were in Whale Bay age-0 herring; this may reflect the proximity of this site to GOA connections via the south-west passages and Montague Strait. Transport of carbon into PWS via Montague Strait rather than Hinchinbrook Entrance (Niebauer et al., 1994) is also suggested by summer PWS surface-water circulation patterns (Vaughan et al., 2001; this volume p. 58). The occurrence of oceanic zooplankton (Foy, unpublished data) within PWS provides further evidence for the role of allochthonous production in PWS. While we can infer that having GOA as an additional source of food during times of local depletion is essential to survival of juvenile herring, a definitive cause and effect relationship could not be detected within the limited scope of the project.

#### Energetics

Age-0 herring metamorphose after the spring zooplankton bloom in July. After metamorphosis they have attained a WBEC measurement of 2–3 kJ g<sup>-1</sup> wet weight (Paul and Paul, 1998b). The timing of metamorphosis allows only a very short growing season in which age-0 herring can prepare for their first winter. This leads to our second hypothesis that it is vital for age-0 herring to achieve a minimal condition during the summer. Seasonal changes in the WBEC occurred for both age-0 and age-1 herring, though the energy content was consistently lower in the younger age group. When fish from all capture sites in all bays were averaged, the WBEC of age-0 fish had similar seasonal changes in all years of this study (Fig. 9f). In August, the mean energy density of age-0 herring was about 3.5 kJ g<sup>-1</sup> wet wt whereas for age-1 herring, energy density was about 5.5 kJ g<sup>-1</sup> wet wt. Both age groups continued to accumulate energy at approximately the same rate from August through October. For the autumn of 1995, age-0 fish had an average of 5.7 kJ g<sup>-1</sup> wet weight vs. 8.0 for age-1 and 9.4–10.2 kJ g<sup>-1</sup> wet weight for ages 2–7 (Paul et al., 1998).

WBEC then decreased throughout the winter months, at a time when stomachs were often empty (Fig. 9d). The lowest values (3.5–4.0 kJ g<sup>-1</sup> wet weight) for young-of-the-year herring were in February and March (Fig. 9f)

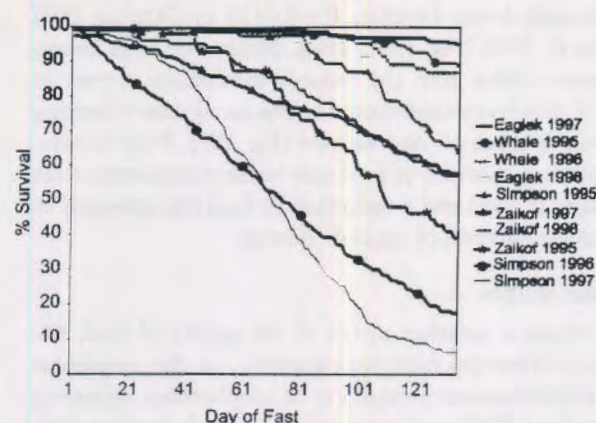


and remained the same or increased slightly in April when the percentage of herring feeding increased. The WBEC values of age-1 juveniles were somewhat greater than those of age-0 herring in March ( $4.5 \text{ kJ g}^{-1}$  wet weight), and spring WBEC values of herring ages 2–7 were even higher ( $> 5 \text{ kJ g}^{-1}$  wet weight; Paul *et al.*, 1998). As the spring and summer progressed, the WBEC of the younger juveniles (now age-1) increased to about  $6.0 \text{ kJ g}^{-1}$  wet weight by June/July while the older juveniles (now age-2) had only a slightly higher WBEC ( $> 6.5 \text{ kJ g}^{-1}$  wet weight). Thus, 3 years of similar mean values of WBEC for age-0 and age-1 herring support the earlier conclusion by Paul *et al.* (1998a) that, compared with older fish, the first 2 years in the life history of herring are more at risk to over-winter mortality because of low energy stores.

The large ranges of size and WBEC in October (Fig. 10a,e) indicate that age-0 herring at different capture sites were not equally prepared for surviving their first winter (Paul and Paul, 1999), thus supporting our third hypothesis that nursery areas vary in quality. Length of fish appeared to be related to energy of herring. In October 1995, the WBEC and length of age-0 fish in Zaikof Bay (Fig. 10a,e) were significantly less (Mann-Whitney rank sum test,  $P < 0.0001$ ) than those found in Whale or Simpson Bays. In October 1996, Eaglek, Whale and Zaikof Bays had similar size herring and WBEC values, but the WBEC value was significantly lower (Mann-Whitney rank sum test,  $P < 0.0001$ ) for the smaller fish in Simpson Bay. The greatest variation of October values of WBEC among bays was in 1997. Herring in Eaglek Bay had significantly greater (Mann-Whitney rank sum test,  $P < 0.0001$ ) WBEC and mean length than herring in Simpson and Zaikof Bays. In general, the energy-dense fish were also the largest fish. However, energy-dense fish were not found in the same bay each year (Fig. 10e), perhaps indicating that no one bay was routinely the optimal nursery area.

Our fourth hypothesis was that survival the first winter, which we linked to condition in hypothesis 2, is key to subsequent year-class strength. Laboratory studies show that fish held without feeding from December through April had a mean WBEC value that decreased from  $5.2$  to  $3.2 \text{ kJ g}^{-1}$  wet weight (Paul and Paul, 1998a). Field collections verify a slow, continual decline in WBEC of age-0 herring from November 1996 ( $5.0 \text{ kJ g}^{-1}$  wet weight) to March 1997 ( $3.9 \text{ kJ g}^{-1}$  wet weight) (Fig. 9f; Foy and Paul, 1999). Age-0 herring that died during laboratory fasts had WBEC values ranging from  $2.8$  to  $3.6 \text{ kJ g}^{-1}$  wet wt. Fish that are shorter than  $80 \text{ mm}$  at the start of winter disappeared during winter, probably due to mortality related to insufficient energy reserves for fasting, fighting disease, and avoiding predators (Paul

**Figure 11.** Results of over-wintering energetics model predicting proportional total over-winter survival of fasting age-0 Pacific herring for bays and years for which both field measurements of October herring whole body energy content and average winter water temperature were available. Time frame is 22 October through 5 March.



and Paul, 1998a; Foy and Paul, 1999). Herring may be highly vulnerable to predators during the winter, as hunger suppresses their antipredatory behaviour (Robinson and Pitcher, 1989; Pitcher and Parrish, 1993; Robinson, 1995; Stokesbury *et al.*, 2000).

In addition to field and laboratory data, an energetics model was developed to evaluate and predict over-winter survival of age-0 herring (Patrick, 2000). Additionally, the model was used to identify the importance of nutritional state and environment on survival. Using field values from October WBEC for individual fish (averages shown in Fig. 10e) and winter water temperatures, the model estimates changes in lipid and protein and their effect on survival rates over a 135-day fasting period. Probability of herring survival varied among the 3 years and four bays sampled (Fig. 11). Survival from October to March ranged from 39% to 86% in 1995–96, 18% to 86% in 1996–97, and 5–95% in 1997–98. Eaglek and Whale Bays consistently had average survival rates of 86% over the three years. Survival in Zaikof Bay ranged from 39% to 56% (mean = 50%). Simpson Bay survival had both the most variable and the lowest survival, ranging from 5% to 64% (mean = 29%). The model predicted survival in the same order of magnitude as acoustic measures of density in winter 1997–98. In Simpson Bay, 5% were predicted to survive and 8% survival was measured (Table 1), whereas the fit was not as close for Zaikof Bay where 56% were expected to survive and 17% were measured. The variability in survival across bays is consistent with our fifth hypothesis that the quality of nursery areas affects the condition and year-class strength of herring.



The over-winter model (Patrick, 2000) illustrates the degree to which nutritional stress has the potential to regulate herring survival. The model shows that autumn energy condition has a greater effect on survival than water temperature. For a winter duration of 120 days, a  $\pm 2^\circ\text{C}$  change in average temperature was inversely equal to  $\pm 15$  days of survival time. Thus temperature was not a significant factor in overall survival except in cases where survival declined at a steep rate (Fig. 11) and when there was less than 10% overall survival as in Simpson Bay 1997–98. These results identify specific bays with low expected survival where it would be important to monitor actual winter water temperatures. Furthermore, the model demonstrates that the length of the winter, i.e. the amount of time in which age-0 herring are not feeding, may be critical to survival. For example, the survival rates after 90 days of winter fasting range from 30% to 98% (Fig. 11). For the smallest age-0 herring, which incur significant over-winter mortality, feeding in March (Fig. 9d) may be critical to survival.

Although the over-winter model does not incorporate a density-dependent factor, competition for food within individual bays is a likely factor affecting survival. If one assumed negligible migration out of the bays, then one could infer the mortality of juvenile herring was not equal within all bays in PWS. In 1996–97 and 1997–98, Simpson Bay had the greatest density of age-0 herring (Table 1) consistent with retention in the eastern region from the larval drift model (Norcross *et al.*, unpublished data). In those 2 years, that bay also had the smallest fish (Fig. 10a), the lowest energy density (Fig. 10f), and the lowest predicted over-winter survival (Fig. 11). The longer fish with the greater WBEC in Simpson Bay in 1995–96 (Fig. 10a,f) resulted in a higher (64%) modelled survival. Unfortunately, there were no acoustic estimates of density for comparison. When considering the idea that quantity rather than quality of food is important in October, one is led to speculate about the size of the forage base, competition within nursery areas and effects on survival.

## SYNTHESIS

The northern location of PWS ( $60^\circ$ – $61^\circ\text{N}$ ), affected by extreme seasonal light and temperature cycles, together with its deep bays and fjords make it a unique nursery area for juvenile Pacific herring. Herring in PWS are genetically distinct from those of Bristol Bay, Alaska (Grant, 1981; Fried and Wespestad, 1985), the only other population of Pacific herring at a similar latitude in North America. Additionally, the geomorphology of Bristol Bay is open bays and long sloping shallow bottom, quite unlike PWS. The geomorphology of PWS is similar

to that of South-east Alaska and British Columbia. Also there is a strong correlation in recruitment time series between PWS and South-east Alaska (Williams and Quinn, 1998). However, the temperature and light effects of the northern location are not as extreme in these southern areas. SEA provided a unique opportunity to study juvenile Pacific herring in this semi-enclosed and apparently separate location of PWS.

Increased water temperature in the summer may enhance feeding rates and promote growth, while warm winter temperature appears to be associated with reduced average size and survival of age-0 herring. This could be a result of increased metabolic demands caused by the warm water (Blaxter and Holliday, 1963). An analogous situation exists in larval herring which use yolk sac resources faster at warmer temperatures and are more susceptible to starvation (McGurk, 1984). Thus, it seems that in PWS a warm summer followed by a cool winter would promote the largest growth and survival in juvenile herring.

The over-wintering energetics model is driven less by temperature than by stored energy, which is the determining factor of winter survival of age-0 herring (Foy and Paul, 1999). Initially we hypothesized that feeding during the summer was critical to over-winter survival and that juvenile herring do not feed during the winter. In actuality, we learned that at no time do all herring juveniles have empty stomachs. The percentage of empty stomachs was always less than 50% except in December. This suggests over-winter feeding by juvenile herring may be an important supplement of stored energy for over-wintering PWS juvenile herring. Furthermore, the energetics model assumes that the fish are not feeding during the winter. Given that some feeding occurs over winter, potential survival may be better than predicted.

The availability of food is thus key to successful survival of juvenile herring. In the past, the attitude may have been parochial, i.e. food availability is contingent upon local conditions. This study shows that in 1995, the major source of carbon in the diets of juvenile herring was from the GOA, proving that conditions outside of PWS can directly affect herring inside PWS. From this short time series, we were not able to learn if presence of GOA carbon in 1995 was normal or an anomaly. This is of particular interest as it is now apparent that the GOA zooplankton biomass varies dramatically at decadal time scales (Brodeur and Ware, 1992).

Though the effects of GOA influx of food appear almost uniformly throughout PWS, the estimated survival of juvenile herring is not equal in all areas. For 1996–97 and 1997–98, modelled survival in Simpson Bay is much lower than in the other bays. Simultaneously, the relative abundance of herring in Simpson Bay



was an order of magnitude higher than that of the other bays, the fish were shorter and had low WBEC, suggesting density-dependence. Though there were higher survival rates in the other bays, there were fewer juvenile herring in those bays. Thus, within-bay competition for food may be an additional factor in the quality of the nursery.

Measurements of temperature, zooplankton abundance, size of juvenile herring, WBEC, energy source (GOA vs. neritic zooplankton) and diet energy show that habitat conditions in various bays and fjords of PWS are not uniformly equal in space and time. The result is that survival is not equally good among nursery areas, or in the same nursery area in all years. This inequality in survival may be linked to interannual variation in local climate and oceanographic conditions (Gay and Vaughan, 1998; 2001; this volume p. 159).

The quality of the nursery area is not linked to a specific area, i.e. the highest quality nursery area is not consistently in the same region each year. The unique nature of each bay presents difficulty for monitoring survival. Additional research is needed to show that the four bays we studied are representative of oceanographic regions within PWS that have similar conditions. The length and WBEC of age-0 herring in March reflect both the quality of growing conditions during the first summer and the severity of winter and therefore provide cumulative estimates of conditions within a bay. A test of this regional hypothesis would be to sample herring condition in March in additional bays within the regions. If specific bays are representative of the regions, then a limited program could easily be developed that monitors condition of age-0 herring in key areas in the autumn. The autumn measurements could then be included in the over-winter model to provide a regional estimate of survival potential for juvenile herring.

## ACKNOWLEDGEMENTS

We wish to thank the many scientists and technicians from UAF, ADFG and PWSSC and fishermen from Cordova, along with Cordova Air, who participated in the field collections. We especially want to thank Ted Cooney and Jennifer Allen for their help and encouragement. We would also like to thank the other SEA investigators, their staffs and students for all their assistance and collaboration. We appreciate the review of this manuscript by R.T. Cooney, D. Hay, B. Holladay, J. Kirsch, C.N.K. Mooers, S. Thornton, S.L. Vaughan and two anonymous reviewers. The Exxon Valdez Oil Spill Trustee Council through the Sound Ecosystem Assessment project funded this project. The findings presented by the authors are their own and not necessarily the Trustee

Council position. Institute of Marine Science Contribution #2693.

## REFERENCES

- Biggs, E.D. and Baker, T.T. (1993) Studies on Pacific herring, *Clupea pallasii*, spawning in Prince William Sound following the 1989 Exxon Valdez oil spill, 1989–92. *Annual Report for Natural Resource Damage Assessment Fish/Shellfish Study Number 11*, Exxon Valdez Oil Spill Trustee Council, Anchorage, Alaska.
- Biggs, E.D., Haley, B.E. and Gilman, J.M. (1992) Historic database for Pacific herring in Prince William Sound, Alaska, 1973–1991. *Regional Informational Report 2C91-11* Department of Fish and Game, Division of Commercial Fisheries, Anchorage, Alaska.
- Bishop, M.A. and Green, P.G. (2001) Predation on Pacific herring (*Clupea pallasii*) spawn by birds in Prince William Sound, Alaska. *Fish. Oceanogr.* 10(Suppl. 1):149–158.
- Blaxter, J.H.S. and Holliday, E.G. (1963) The behavior and physiology of herring and other clupeids. *Ad. Mar. Biol.* 1:261–393.
- Brady, J.A. (1987) Distribution, Timing, Relative Biomass Indices for Pacific Herring as Determined by Aerial Surveys in Prince William Sound 1978–87. *Prince William Sound Data Report no. 87-14*. Alaska Department of Fish and Game, Division of Commercial Fisheries, Juneau, AK.
- Brady, J., Morstad, S., Simpson, E. and Biggs, E. (1991) *Prince William Sound area annual finfish management report 1989. Regional Information Report no. 2C90-07*. Cordova, AK: Alaska Department of Fish and Game.
- Brodeur, R. and Ware, D. (1992) Long-term variability in zooplankton biomass in the subarctic Pacific Ocean. *Fish. Oceanogr.* 1:32–38.
- Brown, E.D. and Borstad, G.A. (1998) Progress report on aerial survey development. Chapter 10, Juvenile herring growth and habitats (Restoration Project 97320T), SEA97 Annual Report, Alaska Department of Fish and Game, Anchorage, AK, 10–60–10–79.
- Brown, E.D., Norcross, B.L. and Short, J.W. (1996) An introduction to studies on the effects of the Exxon Valdez oil spill on early life history stages of Pacific herring, *Clupea pallasii*, in Prince William Sound, Alaska. *Can. J. Fish. Aquat. Sci.* 53:2337–2342.
- Brown, E.D., Seitz, J., Norcross, B.L. and Huntington, H.P. (in press) Ecology of herring and other forage fish as recorded by resource users of Prince William Sound and the Outer Kenai, Alaska. *Alaska Fish. Res. Bull.*
- Brown, E.D., Wang, J., Vaughan, S.L. and Norcross, B.L. (1999) Identifying seasonal spatial scale for the ecological analysis of herring and other forage fish in Prince William Sound, Alaska. *Ecosys. Appr. Fish. Mgmt.* AK-SG-99-01, pp. 499–510.
- Carlson, H.R. (1980) Seasonal distribution and environment of Pacific herring near Auke Bay, Lynn Canal, Southern Alaska. *Trans. Am. Fish. Soc.* 109:71–78.
- Cooney, R.T., Allen, J.R., Bishop, M.A., Eslinger, D.L., Kline, T., Norcross, B.L., McRoy, C.P., Milton, J., Olsen, J., Patrick, V., Paul, A.J., Salmon, D., Scheel, D., Thomas, G.L., Vaughan, S.L., and Willette, T.M. (2001a) Ecosystem controls of juvenile pink salmon (*Oncorhynchus gorbuscha*) and Pacific herring (*Clupea pallasii*) populations in Prince William Sound, Alaska. *Fish. Oceanogr.* 10(Suppl. 1):1–13.



- Cooney, R.T., Coyle, K.O., Stockmar, E. and Stark, C. (2001b) Seasonality in surface-layer net zooplankton communities in Prince William Sound, Alaska. *Fish. Oceanogr.* 10(Suppl. 1):97–109.
- Cushing, D.H. (1975) *Marine Ecology and Fisheries*. London: Cambridge University Press.
- Eslinger, D.L., Cooney, R.T., McRoy, C.P., Ward, A., Kline, T., Simpson, E.P., Wang, J. and Allen, R.J. (2001) Plankton dynamics: observed and modelled responses to physical conditions in Prince William Sound, Alaska. *Fish. Oceanogr.* 10(Suppl. 1):81–96.
- Foy, R.J. and Norcross, B.L. (1999a) Feeding behavior of herring (*Clupea pallasii*) associated with zooplankton availability in Prince William Sound, Alaska. *Ecosystem Consideration in Fisheries Management. Proceedings of the International Symposium on Ecosystem Consideration in Fisheries Management*. Alaska Sea Grant College Program Report no. 99–01. University of Alaska Fairbanks, Alaska, 129–135.
- Foy, R.J. and Norcross, B.L. (1999b) Spatial and temporal differences in the diet of juvenile Pacific herring (*Clupea pallasii*) in Prince William Sound, Alaska. *Can. J. Zool.* 77:697–706.
- Foy, R.J. and Paul, A.J. (1999) Winter feeding and changes in somatic energy content for age-0 Pacific herring in Prince William Sound, Alaska. *Trans. Am. Fish. Soc.* 128:1193–1200.
- Fried, S.M. and Wespestad, V.G. (1985) Productivity of Pacific herring (*Clupea harengus pallasii*) in the eastern Bering Sea under various patterns of exploitation. *Can. J. Fish. Aquat. Sci.* 42 (Suppl. 1):181–191.
- Funk, F. (1994) Forecast of the Pacific herring biomass in Prince William Sound, Alaska, 1993. *Regional Information Report no. 5J94-04*, Juneau, AK: Alaska Department of Fish and Game.
- Funk, F. and Harris, M. (1992) Preliminary Forecasts of Catch and Stock Abundance for 1992 Alaska Herring Fisheries. *Regional Information Report no. 5J92-04*, Juneau, AK: Alaska Department of Fish and Game.
- Gay III, S.M. and Vaughan, S.L. (1998) Descriptive physical oceanography of bays and fjords in Prince William Sound, Alaska used as nursery habitat by juvenile Pacific herring (*Clupea pallasii*). Exxon Valdez Oil Spill Restoration Project Annual Rep. (Restoration Project 96320-M.) Cordova, Alaska: Prince William Sound Science Center, No. 8:94–165.
- Gay III, S.M. and Vaughan, S.L. (2001) Seasonal hydrography and tidal currents of bays and fjords in Prince William Sound, Alaska. *Fish. Oceanogr.* 10(Suppl. 1):159–193.
- Grant, S. (1981) *Biochemical Genetic Variation, Population Structure and Evolution of Atlantic and Pacific Herring*. PhD Thesis. University of Washington, Seattle, WA.
- Haegele, C.W. (1994) Juvenile herring surveys (1990–93) in the Strait of Georgia. *Proceedings of the Seventh Pacific Coast Herring Workshop*, January 27–28, 1994. *Can. Tech. Rpt. Fish. Aquat. Sci.* 2060:23–37.
- Hay, D.E. (1985) Reproductive biology of Pacific herring (*Clupea harengus pallasii*). *Can. J. Fish. Aquat. Sci.* 42(Suppl. 1):111–126.
- Hay, D.E. and McCarter, P.B. (1997) Continental shelf area and distribution, abundance, and habitat of herring in the North Pacific. *Proc. Forage Fish Mar. Ecosys. Symp.*, AK-SG-97–01, pp. 559–572.
- Iles, T.D. and Sinclair, M. (1982) Atlantic herring: stock discreteness and abundance. *Science* 215:627–633.
- Kline, T.C. Jr (1997) Confirming forage fish food web dependencies in Prince William Sound using natural stable isotope tracers. *Forage Fishes in Marine Ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems*. Alaska Sea Grant College Program Report no. 97–01. University of Alaska Fairbanks, Alaska, 257–269.
- Kline, T.C. Jr (1999a) Temporal and spatial variability of  $^{13}\text{C}$ / $^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$  in pelagic biota of Prince William Sound, Alaska. *Can. J. Fish. Aquat. Sci.* 56(Suppl. 1):94–117.
- Kline, T.C. Jr (1999b) Monitoring changes in oceanographic forcing using the carbon and nitrogen isotopic composition of Prince William Sound pelagic biota. *Ecosystem Consideration in Fisheries Management. Proceedings of the International Symposium on Ecosystem Consideration in Fisheries Management*. Alaska Sea Grant College Program Report no. 99–01. University of Alaska Fairbanks, Alaska, 87–95.
- McGurk, M.D. (1984) Effects of delayed feeding and temperature on the age of irreversible starvation and on the rates of growth and mortality of Pacific herring larvae. *Mar. Biol.* 84:13–26.
- McGurk, M.D., Paul, A.J., Coyle, K.O., Ziemann, D.A. and Halderson, L.J. (1993) Relationships between prey concentration and growth, condition, and mortality of Pacific herring, *Clupea pallasii*, larvae in an Alaskan subarctic embayment. *Can. J. Fish. Aquat. Sci.* 50:163–180.
- McRoy, C.P., Ward, A., Simpson, E.P., Clayton, D., Cameron, J., McCullough, S. and Suring, E. (1997) Sound Ecosystem Analysis: phytoplankton and nutrients. *Exxon Valdez Oil Spill Restoration Project Annual Report (Restoration Project 96320G)*, Alaska. Department of Fish and Game, Anchorage, Alaska, pp. 3–1–3–29.
- Niebauer, H.J., Royer, T.C. and Weingartner, T.J. (1994) Circulation of Prince William Sound, Alaska. *J. Geophys. Res.* 99:113–126.
- Norcross, B.L. and Brown, E.D. (in press) Estimation of first year survival of Pacific herring from a review of recent stage-specific studies. In *Herring: Expectations for a New Millennium*. F. Funk, J. Blackburn, D. Hay, A.J. Paul, R. Stephenson, R. Toresen and D. Witherell (eds). Fairbanks, Alaska: University of Alaska Sea Grant, AK-SG-01–04.
- Norcross, B.L., Hose, J.E., Frandsen, M. and Brown, E.D. (1996) Distribution, abundance, morphological condition, and cytogenetic abnormalities of larval herring in Prince William Sound, Alaska, following the Exxon Valdez oil spill. *Can. J. Fish. Aquat. Sci.* 53(10):2376–2387.
- Patrick, E.V. (2000) Evolution equation models for the advective transport during spring and the fasting physiology during winter of age-0 Pacific herring in Prince William Sound, Alaska. *Results from projects J, U, T and I of the Sound Ecosystem Assessment Program*. ISR Technical Report 2000–12, Institute for Systems Research, University of Maryland, College Park, MD.
- Patrick, E.V., Mason, D.M., Foy, R.J., Norcross, B.L., Paul, A.J., Stokesbury, K.D.E., Kline Jr, T.C. (in press) Sound Ecosystem Assessment (SEA): Model for the physiology and survival of age-0 Pacific herring during winter fasting. *Fish. Oceanogr.*
- Paul, A.J. and Paul, J.M. (1998a) Comparisons of whole body energy content of captive fasting age zero Alaskan Pacific herring (*Clupea pallasii* Valenciennes) and cohorts overwintering in nature. *J. Exp. Mar. Biol. Ecol.* 226:75–86.
- Paul, A.J. and Paul, J.M. (1998b) Spring and summer whole body energy content of Alaskan juvenile Pacific herring. *Alaska Fish. Res. Bull.* 5:131–136.



- Paul, A.J. and Paul, J.M. (1999) Interannual and regional variations in body length, weight and energy content of age-0 Pacific herring from Prince William Sound, Alaska. *J. Fish Biol.* 54:996–1001.
- Paul, A.J., Paul, J.M. and Brown, E.D. (1998) Fall and spring somatic energy content for Alaskan Pacific herring (*Clupea pallasii* Valenciennes 1847) relative to age, size and sex. *J. Exp. Mar. Biol. Ecol.* 223:133–142.
- Pitcher, T.J. and Parrish, J.K. (1993) Functions of shoaling behaviour in teleosts. *Behaviour of Teleost Fishes*. In: T.J. Pitcher (ed.). New York: Chapman & Hall, pp. 363–439.
- Robinson, C.J. (1995) Food competition in a shoal of herring: the role of hunger. *Mar. Behav. Physiol.* 24:237–242.
- Robinson, C.J. and Pitcher, T.J. (1989) Hunger motivation as a promoter of different behaviors within a shoal of herring: selection for homogeneity in fish shoal? *J. Fish. Biol.* 35:459–460.
- Rooper, C.N. (1996) *Physical and Biological Factors Affecting Pacific Herring Egg Loss in Prince William Sound, Alaska*. MSc Thesis, University of Alaska Fairbanks, Alaska.
- Rooper, C.N., Haldorson, L.J. and Quinn, T.J.I.I. (1999) Habitat factors controlling Pacific herring (*Clupea pallasii*) egg loss in Prince William Sound, Alaska. *Can. J. Fish. Aquat. Sci.* 56:1133–1142.
- Rounsefell, G. and Dahlgren, E.H. (1931) Fluctuations in the supply of herring (*Clupea pallasii*) in Prince William Sound, Alaska. U.S. Department of Commerce, Bureau of Fisheries Doc. no. 9. 263–291.
- Sinclair, M. (1988) Marine populations: an essay on population regulation and speciation. *Washington Sea Grant Program*. Seattle, WA: University of Washington Press.
- Sinclair, M. and Iles, T.D. (1985) Atlantic herring (*Clupea harengus*) distributions in the Gulf of Maine – Scotian Shelf area in relation to oceanographic features. *Can. J. Fish. Aquat. Sci.* 42:880–887.
- Stokesbury, K.D.E., Foy, R.J. and Norcross, B.L. (1999) Spatial and temporal variability in juvenile Pacific herring (*Clupea pallasii*) growth in Prince William Sound, Alaska. *Environ. Biol. Fish.* 56:409–418.
- Stokesbury, K.D.E., Kirsch, J., Brown, E.D., Thomas, G.L. and Norcross, B.L. (2000) Seasonal variability in Pacific herring (*Clupea pallasii*) and walleye pollock (*Theragra chalcogramma*) spatial distributions in Prince William Sound, Alaska. *Fish. Bull. (US)* 98:400–409.
- Stokesbury, K.D.E., Kirsch, J. and Norcross, B.L. (in press) Natural mortality estimates of juvenile Pacific herring (*Clupea pallasii*) in Prince William Sound, Alaska. *Can. J. Fish. Aquat. Sci.*
- Tanisichuk, R.W., Kristofferson, A.H. and Gillman, D.V. (1993) Comparison of some life history characteristics of Pacific herring (*Clupea pallasii*) from Canadian Pacific Ocean and Beaufort Sea. *Can. J. Fish. Aquat. Sci.* 50:964–971.
- Taylor, F.H.C. (1964) Life history and present status of British Columbia herring stocks. *Bull. Fish. Res. Board Can.* 143:81.
- Vaughan, S.L., Christopher, N.K., Mooers, S.M. and Gay III, S.M. (2001) Physical variability in Prince William Sound during the SEA Study (1994–98). *Fish. Oceanogr.* 10(Suppl. 1): 58–80.
- Wang, J., Mooers, C.N.K. and Patrick, E.V. (1997) A three dimensional tidal model for Prince William Sound, Alaska. *Computer Modelling of Seas and Coastal Regions*. In: J.R. Acinas III and C.A. Brebbia (eds). Southampton: Computational Mechanics Publications, 95–104.
- Wang, J., Jin, M., Patrick, E.V., Allen, J.R., Eslinger, D.L. and Cooney, R.T. (2001) Numerical simulations of the seasonal circulation patterns and thermohaline structures of Prince William Sound, Alaska. *Fish. Oceanogr.* 10(Suppl. 1):132–148.
- Willette, M., Carpenter, G., Hyer, K. and Wilcock, J. (1998) *Herring Natal Habitats. Final Report for Restoration Project 97166 to the Exxon Valdez Oil Spill*. Anchorage, Alaska: Exxon Valdez Oil Spill Trustee Council.
- Williams, E.H. and Quinn, T.J.I.I. (1998) Pacific herring, *Clupea pallasii*, population associations in the Bering Sea and Gulf of Alaska based on recruitment time series. Appendix 3. In: E.H. Williams, T.J. Quinn II and L.J. Haldorson (eds). *Herring Natal Habitats: Project Number 97166, Analysis of Recruitment of Pacific Herring. Final Report*. Anchorage, Alaska: Exxon Valdez Oil Spill Trustee Council.